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Field attraction of Coleoptera to odours of the wood-decaying polypores *Fomitopsis pinicola* and *Fomes fomentarius*

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The attraction of beetles (Insecta: Coleoptera) to odours of the wood-decaying polypore fungi *Fomitopsis pinicola* and *Fomes fomentarius* was studied at one spruce-dominated and one birch-dominated locality in a semi-natural forest in central Sweden. Beetles were caught in window traps without a bait (control) or baited with chopped, living fruiting bodies of either of the two polypores. The pattern of attraction was analyzed for 96 taxa, which were assigned to different categories according to the substrate they utilize. The attraction patterns were compared with catch data from window traps beneath living fruiting bodies and with rearing data. Beetles of the family Cisidae breeding in *F. pinicola* were strongly attracted to the odour of this fungus. In contrast, the species of a similar cisid guild associated with *F. fomentarius* was not attracted to any of the fungal odours. Two monophagous species of the anobiid genus *Dorcatoma* associated with *F. pinicola* and *F. fomentarius* respectively, were not significantly attracted to odour host but were caught in large numbers at living fruiting bodies. This aggregation was probably due to response to attractive pheromones. Knowledge about the precision in orientation as well as the capacity of dispersal of these insects is considered important for evaluating how they are affected by forestry practices.

1. Introduction

Forest management in northern Europe has been very intensive during the last decades. Consequently, populations of many organisms associated with dead trees and decaying wood have been declining as the availability of their breeding substrate has decreased (Esseen et al. 1992, Haila 1994, Siitonen & Martikainen 1994). A large number of these species are now considered threatened or vulnerable. For instance, no fewer than 508 wood-living beetles have been placed on the Swedish Red List (Ehnström et al. 1993). To optimize measures for conserving species we need relevant knowledge about their biology. Our knowledge concerning the types of substrates utilized by various beetle species associated with dead wood and wood-living fungi is fairly good (Palm 1959, Berg et al. 1994). However, little is known about their dispersal capacities and abilities to locate breeding sites, as is true for patchily distributed insects in general, especially rarer species (Hansson et al. 1992).

Wood-decaying fungi extract and concentrate nutrients from the wood. Thus, for the insects these fungi may serve as a higher quality source of food than the wood itself (Martin, 1979). Of the beetle species inhabiting bark or wood of deciduous trees in Sweden, at least 35% (257 species) feed on fungi (Palm 1959). The most important and conspicuous group of wood-decaying fungi are the polypores, which have a diverse fauna of associated insects, consisting mainly of Coleoptera and Diptera (Hanski 1989). In Finland, 234 species of beetles associated with dead wood or wood-living fungi were caught in window traps attached beneath fruiting bodies of polypores (Kaila 1993). Although most fungivorous insects are polyphagous, the species living on perennial fruiting bodies of the polypores tend to be more host-species specific (Hanski 1989).

In general, fruiting bodies of perennial polypores only provide insects suitable breeding substrate when they are in the process of dying and for one or a few years after their death (Mathewman & Pielou 1971, Lawrence 1973). However, the fruiting bodies on a tree trunk do not usually all die simultaneously. This means that a given trunk may provide a suitable patch for insects colonizing dying fruiting bodies for more than a decade. The colonization of such patches is not likely to be limited by the dispersal capacity of the insects in a natural forest where dead wood and wood-decaying fungi are abundant. However, the capacity of dispersal may become limiting for many species in intensively managed forests where the production of the resource required by the insects has been disrupted. The success with which the insects find breeding substrate in a given environment should be largely determined by their flight capacity and ability to orient to suitable substrate while flying.

This paper deals with the orientation component in the colonization process. We compare the extents to which different beetle species respond in flight to the odours from fruiting bodies of two common decay fungi, the polypores *Fomitopsis pinicola* Fr. (Karst.) and *Fomes fomentarius* (L. ex Fr.) Kickx. Little is known about the degree to which olfactory cues are used by insects searching for fruiting bodies of polypores. No insect species associated with *F. pinicola* were attracted in significant numbers to traps baited with fruiting bodies of this species in a recent Norwegian study (Økland & Hågvar 1994). Paviour-Smith (1960) doubted that beetles of the family Cisidae are attracted to host odours, since these beetles are found only in dead fruiting bodies. Lawrence (1973) speculated that pioneer cisid beetles find the fruiting bodies by chance and that conspecifics are then attracted to a pheromone. There are, however, examples of insects being attracted to volatiles of their fungal hosts. The odours from truffles were analysed by Pacioni et al. (1990) and some of the components found were then used in an attraction experiment in the field. It was found that leiodids and staphylinids (Coleoptera) as well as some species of Lepidoptera and Diptera were attracted to dimethyl sulphide (Pacioni et al. 1991). Many insects living in stored products or fruits have also been shown to be attracted to fungal-derived volatiles (Honda et al. 1988, Phelan & Lin 1991, Pierce et al. 1991).

The main objectives of the present study were to determine whether various beetle species inhabiting the fruiting bodies of *F. pinicola* or *F. fomentarius* orient in flight to the odours of these species in the field and to ascertain how specific they are in their orientation. We also wanted to determine the extent to which other beetles associated with fungi or dead wood are attracted by the same odours. This study forms part of an ongoing project dealing with the insect fauna of perennial polypores, with emphasis on assessing the impacts of past and present forest-management practices on populations of these insects.

2. Materials and methods

Attraction of beetles to chopped fruiting bodies of the two polypores *F. pinicola*, and *F. fomentarius* was tested in a trapping experiment. Both species are very common in Swedish forests, but differ in their host-tree preferences. *Fomitopsis pinicola* primarily infects Norway spruce (*Picea abies*) but also is rather frequent on Scots pine (*Pinus sylvestris*), birches (*Betula* spp.), and several other tree species. In central Sweden, *F. fomentarius* grows mainly on birches, but occurs on some related trees, e.g. *Alnus* spp., and *Populus* spp., as well (Ryman and Holmåsen 1984).

The trapping experiment was carried out between April 28 and September 29, 1993, at two localities separated by 4 km within a forest area, Lunsen, SSE of Uppsala, Sweden. The first locality was an old, spruce-dominated forest, where *F. pinicola* was very common. The second locality was a birch-dominated forest where *F. fomentarius* was the most abundant polypore species. However, both species occurred at both localities. Since dead trees and logs were abundant in both areas, the densities of polypores were very high. These localities were chosen because they were known to contain large populations of many insect species associated with the two fungi.

Window traps were arranged in 12 blocks at each of the two localities. Each block consisted of one trap with a *F. pinicola*-bait, one with a *F. fomentarius*-bait, and one empty control trap. Thus, there were 72 traps in total. Traps within a block were placed in a triangle, with about 10 m between traps, and the blocks were separated by at least 20 m. No logs with a diameter larger than 10 cm were allowed closer than 10 m from any trap. The traps consisted of a PVC window (width 35 cm, height 50 cm) nailed to two wooden poles, with the top of the window 1.5 m above ground. Under the window was a jar in which intercepted insects were captured. The jar had an 18 × 18 cm opening and contained water with a small amount of detergent added. The odour baits consisted of chopped and well-mixed fruiting bodies of the polypores placed in a metal tube with a fine metal mesh at both ends. Each tube contained 0.3 l of chopped fruiting bodies and was hung in an opening in the window. The traps were emptied every week, while the odour bait was renewed every second week. One or two days before renewal, living fruiting bodies without visible insect attacks were collected at various localities around Uppsala. *F. pinicola* was always collected from spruce and all *F. fomentarius* originated from birch. About 36 medium-sized fruiting bodies of each species were chopped and mixed with the aid of a compost mill, and the mixture was then stored in a refrigerator until use.

Data from rearings of insects from fruiting bodies and catches of insects near living fruiting bodies were taken from parallel studies in the same areas. For the rearings, fruiting bodies were collected during late winter or early spring in 1992 and 1993. They were then put into 1-litre containers of waxed paper and kept at room temperature. Each container was provided with an inserted glass vial, in which emerging photopositive insects were captured. Remaining insects were collected by opening the container and dissecting the fruiting bodies after the emergence period.

The abundance of flying insects around living polypores was measuered with small window traps attached on stumps or logs directly beneath the fruiting bodies. Twelve traps under *F. pinicola* at the spruce locality and eight traps under *F. fomentarius* at the birch locality were in operation from May 12 to October 21, 1992. The trap was similar to the trunk window trap described by Kaila (1993), but somewhat simplified. Flying insects were intercepted by a PVC window measuring 20 × 15 cm placed directly above a 5 cm deep aluminium basin with a 15 × 11 cm opening filled with a 50% aqueous solution of etyhlene glycol. Drainage holes were made 3 cm above the bottom to avoid overflow.

Throughout the study all insects were collected, but only the beetles are analysed here. Most collected specimens were identified to species, but in some cases they were only determined to genus or subgenus. The literature relied on most for the identification work was Freude et al. (1965–1994), Hansen (1950,1968, 1973), Lindroth (1933), Strand (1965), Landin (1970), Palm (1948–1972), and Baranowski (1985). The classification and nomenclature follow Silfverberg (1992). The insects were preseved in ethanol or as dried specimens and are deposited at the Department of Entomology, Swedish University of Agricultural Sciences, Uppsala.

Statistical comparisons of catches between treatments were made separately for each taxon at each locality. Only total catches exceeding 15 specimens at a given locality were analysed. Catch numbers were log $(x + 1)$ transformed to obtain normal distributions and equal variances. Differences between treatments were tested with an ANOVA, where the model consisted of bait-type and block-number. Tukey´s test was used for the multiple comparisons. In cases where more specimens of a species were caught at baited traps than at control traps and this difference was significant, we concluded that individuals of this species were attracted in flight to the odour. For comparing catches obtained during the first week after renewal of the odour substrate with those obtained during the second week, confidence-intervals for binomial distributions were used. The distribution of total numbers of individuals caught during each of the two kinds of weeks were used for defining expected values. The test was only made with species caught during at least ten different weeks. In addition, some species were excluded because most of the specimens were caught for only a few weeks.

3. Results

Odour traps with fungal baits caught 1.3 to 2.0 times as many beetle specimens as the empty controls (Table 1). These catch ratios were somewhat higher for *F. pinicola* than for *F. fomentarius*, and also somewhat higher at the spruce locality than at the birch locality. Total numbers of specimens and identified taxa (mainly species) were fairly similar at the two localities. However, 50% of the total number of taxa were recorded from only one of the localities while 50% occurred on both localities. Thus, although the two localities differed considerably in faunal composition, there were only small differences between them regarding the distribution of trapped specimens among the treatments and total numbers of trapped specimens or taxa.

In total, 96 beetle taxa were represented by more than 15 specimens each from at least one of the two localities (Table 2). Of these 96 taxa, 28 showed significant attraction to fungal odour. In the spruce forest, 66 taxa were caught and 20 were attracted, while in the birch forest the corresponding numbers were 66 and 16. Generally, the responses to the various treatments did not differ between sites. When comparing trap catches for the two sites, we did not find any contradictory results that were statistically significant for any of these taxa, and only one species, *Quedius xanthopus*, showed different tendencies. Ten species showing similar patterns in the comparison made between localities were only attracted in significant numbers at one of them. Not a single species was caught in significantly higher numbers in control traps than in traps with fungal baits.

In Table 2 all but one of the taxa were assigned to one of seven substrate-utilization categories, and some categories were further divided with regard to preferred hosts. Species attracted to *F. pinicola*-baited traps included all three species restricted to *F. pinicola* (*Pteryngium crenatum*, *Cis glabratus*, *C. quadridens*), the single species restricted to *F. fomentarius* (*Dorcatoma robusta*) and several species living on other fungi than polypores (Table 3). Some species in the latter group were also attracted to the *F. fomentarius* -baits. In addition, these baits attracted some species living under the decaying bark of hardwood trees. "Beetles associated with perennial polypores" was the only category in which all species preferred baited traps. In all the other categories at least some species did not show any significant responses. In the "decaying wood" category only two out of 12 species were attracted to fungal odour. Among species associated with "recently killed trees" (only bark beetles, Scolytidae) or "other substrates" (litter-dwelling and leaf-eating beetles), not a single species was attracted to baited traps. This was also the case for the three species living on *Trametes,* which are annual polypores.

Primary interest in this study was focused on the attraction of fungivorous beetles that are restricted to polypores. Rearings of insects from fruiting bodies of *F. fomentarius* and *F. pinicola* collected from the spruce and birch localities gave information about the host preferences and local abundance of these species (Table 4). Attraction to the baits consisting of chopped fruiting bodies of *F. pinicola* and *F. fomentarius* was also compared with trapping data from trunk window traps placed beneath fruiting bodies of these two species in the same areas (Table 5). The frequently reared cisids *Cis glabratus* and *C. quadridens* were both strongly attracted to the odour of their host, *F. pinicola*. For these species catch numbers at odour traps were about equal to those in trunk traps. The oligophagous cisid *Ennearthron cornutum* was also attracted to

Table 1. Numbers of beetle specimens and identified beetle taxa (usually species) caught in the odour traps at the spruce and birch localities.

Locality	Odour bait	No. of specimens	Catch ratio: baited traps/ control	Total no. of taxa
Spruce	*F. pinicola*	2147	2.0	173
– ″ –	*F. fomentarius*	1894	1.8	176
– ″ –	Control	1060		136
– ″ –	All traps	5101		237
Birch	*F. pinicola*	1991	1.7	196
– ″ –	*F. fomentarius*	1590	1.3	176
– ″ –	Control	1184		177
– ″ –	All traps	4765		268
Spruce + birch	*F. pinicola*	4138	1.8	265
– ″ –	*F. fomentarius*	3484	1.6	257
– ″ –	Control	2244		252
– ″ –	All traps	9866		337

Table 2. Attraction of beetles to polypore-baited traps at the spruce and birch localities during the period 28 Apr.–29 Sep. 1993. Symbols and abbreviations used for describing attraction patterns: '–' = attraction not analyzed (<16 specimens), '0' = no significant attraction at the 5 % level, 'pi' = significant attraction to *F. pinicola,* 'fo' = significant attraction to *F. fomentarius,* 'pi = fo' = significant attraction to both polypores but no difference between them, 'pi>fo' = significant attraction to both polypores but *F. pinicola* significantly more attractive than *F. fomentarius.* Asterisks denote significance level compared with unbaited control (* = $p < 0.05$, ** = $p < 0.01$, *** $p < 0.001$, Tukey test). Substrate-utilization category: 'P' = polypores, 'F' = fungi other than polypores, 'B' = under decaying bark, 'W' = decaying wood, 'R' = recently killed trees (1st year), 'S' = saprophages; 'O' = other substrates. Hosts: 'pi' = *Fomitopsis pinicola*, 'fo' = *Fomes fomentarius*, 'Tra' = annual polypores (*Trametes*), 'D' = deciduous trees, 'C' = coniferous trees, '–' = host association unknown or ambiguous.

	Total catch		Attraction			
Species	Spruce locality	Birch locality	Spruce locality	Birch locality	Substrate	Host
Calathus micropterus (Dft.)	57		0	–	O	–
Acrotrichis spp.	31	30	0	0	O	–
Anisotoma glabra (Kugel.)	17		fo*	–	F	–
Agathidium varians Beck		38	–	0	F	–
Agathidium seminulum (L.)	21	17	0	0	F	–
Nicrophorus vespilloides Hbst.	52	24	pi***= fo**	0	S	–
Sciodrepoides watsoni (Spence)		19	–	0	S	–
Sciodrepoides fumata (Spence)	44	50	pi** = fo*	pi*** = fo***	S	–
Gabrius splendidulus (Grav.)	26	25	0	0	B	DC
Philonthus succicola Thoms		19	–	0	S	–
Quedius xanthopus Er.	27	22	fo*	0	B	DC
Proteinus brachypterus (F.)	39	36	pi**	pi*	F	–
Acrulia inflata (Gyll.)	35	43	0	fo*	F	–
Hapalarea linearis (Zett.)	29		0	–	F	–
Scaphisoma spp.	47	21	pi* = fo*	0	F	–
Lordithon trinotatus (Er.)	39		pi***	–	F	–
Lordithon lunulatus (L.)	85	80	pi*** > fo**	pi*** >fo*	F	–
Tachinus rufipes (F.)		29	–	0	O	–
Tachinus laticollis Grav.		17	–	0	O	–
Oxypoda alternans (Grav.)	46		pi*	–	F	–
Haploglossa villosula (Steph.)	20		0	–	W	–
Atheta spp.	202	449	pi*** = fo***	pi*** = fo***	?	–
Atheta picipes (Thoms.)		19	–	pi* = fo*	B	DC
Gyrophaena poweri Crotch		92	–	fo*	F	–
Agaricochara latissima (Steph.)		21	–	0	P	Tra
Leptusa pulchella (Mannh.)	21		0	–	B	DC
Leptusa fumida (Er.)		17	–	0	B	DC
Bibloporus bicolor (Denny)	34	42	0	0	B	DC
Euplectus spp.	23		fo**	–	W	DC
Cyphon spp.	20	28	0	0	O	–
Aphodius spp.	27	33	0	0	O	–
Dictyoptera aurora (Hbst.)	25		0	–	W	DC
Malthinus spp.	20		0	–	W	DC
Malthodes spp.	36	44	0	0	W	DC
Malthodes fuscus (Waltl)	26		0	–	W	DC
Malthodes brevicollis (Payk.)	58		0	–	W	DC
Athous haemorrhoidalis (F.)		55	–	0	O	–
Athous subfuscus (Müll)	215	93	0	0	O	–
Ampedus balteatus (L.)	19		0	–	W	DC
Ampedus nigrinus (Hbst.)	34		0	–	W	DC
Sericus brunneus (L,1758)	29		0	–	O	–

(Continued)

Table 2. continued.

Species	Total catch		Attraction		Sub-strate	Host
	Spruce locality	Birch locality	Spruce locality	Birch locality		
Melanotus castanipes (Payk.)	111	35	0	0	W	DC
Dalopius marginatus (L.)	100	313	0	0	O	–
Microrhagus pygmaeus (F.)		27	–	0	W	D
Trixagus dermestoides (L.)		22	–	0	O	–
Dorcatoma robusta Strand		20	–	pi*	P	fo
Ptinus subpilosus Sturm	84		0	–	W	DC
Dasytes plumbeus (Müll)	19	56	0	0	O	–
Meligethes spp		26	–	0	O	–
Glischrochilus hortensis (Geoff.)	49	39	fo*** > pi*	fo** = pi*	B	D
Arpidiphorus orbiculatus (Gyll.)	30	28	0	0	F	–
Rhizophagus dispar (Payk.)		20	–	0	B	DC
Rhizophagus nitidulus (F.)		35	–	0	B	D
Rhizophagus parvulus (Payk.)		164	–	fo*	B	D
Dendrophagus crenatus (Payk.)	69		0	–	B	DC
Pteryngium crenatum (F.)	64		pi*** > fo*	–	P	pi
Cryptophagus spp.	16	51	0	pi*	F	–
Cryptophagus abietis (Payk.)	52		0	–	O	–
Atomaria s. str.	85	48	0	0	F	–
Atomaria subg. *Anchicera*	87	112	0	0	F	–
Triplax aenea (Schall.)		37	–	0	F	–
Triplax russica (L.)	18		0	–	F	–
Cerylon histeroides (F.)	20		0	–	B	D
Cerylon ferrugineum Steph.	46	35	fo*	fo*	B	D
Orthoperus spp.		32	–	0	O	–
Latridius consimilis Mann.		31	–	0	F	–
Enicmus fungicola Thoms.	18	60	0	0	F	–
Enicmus rugosus (Hbst.)	221	56	0	0	F	–
Enicmus testaceus (Steph.)	175	263	pi*	0	F	–
Aridius nodifer (Westwood)		31	–	0	F	–
Corticaria spp.	27		0	–	F	–
Cortinicara gibbosa (Hbst.)		99	–	0	F	–
Corticarina similata (Gyll.)		26	–	0	F	–
Corticarina obfuscata Strand	32		0	–	F	–
Corticarina fuscula (Gyll.)		33	–	pi*	F	–
Cis glabratus Mellié	135		pi***	–	P	pi
Cis hispidus (Payk.)	21	16	0	0	P	Tra
Cis boleti (Scop.)	26	18	0	0	P	Tra
Cis quadridens Mellié	86		pi***	–	P	pi
Ennearthron cornutum (Gyll.)	27		pi**	–	P	–
Schizotus pectinicornis (L.)		16	–	0	B	D
Salpingus planirostris (F.)	16	169	0	pi*	B	D
Salpingus ruficollis (L.)	238	174	fo*** > pi*	pi* = fo*	B	D
Anaspis rufilabris (Gyll.)	572	282	pi*** = fo***	0	W	DC
Xylita laevigata (Hellenius)	72		0	–	W	C
Phyllotreta spp.		33		0	O	–
Chaetocnema spp.		18	–	0	O	–
Anthribus nebulosus Forst.	40		0	–	O	–
Hylastes cunicularius Er.	68	23	0	0	R	C
Phloeotribus spinulosus (Rey)	16		0	–	R	C
Pityogenes chalcographus (L.)	21	76	0	0	R	C

(Continued)

Table 2. continued.

Species	Total catch		Attraction		Sub-strate	Host
	Spruce locality	Birch locality	Spruce locality	Birch locality		
Dryocoetes spp.	26	48	0	0	R	C
Crypturgus spp.	314		0	–	R	C
Trypodendron domesticum (L.)		19	–	0	R	D
Cryphalus spp.		17	–	0	R	C
Pityophthorus micrographus (L.)		65	–	0	R	C

F. pinicola odour, but was not caught in the trunk traps. In contrast to the *F. pinicola* associates, no beetles living on *F. fomentarius* were significantly attracted to the odour traps. Only a few specimens of the cisids *Cis jaquemarti*, *Cis alter*, and *Ropalodontus strandi* and the tenebrionid *Bolitophagus reticulatus* were caught in odour traps and trunk traps. A different pattern of attraction was shown by the two monophagous anobiids *Dorcatoma punctulata* on *F. pinicola* and *D. robusta* on *F. fomentarius*. These species tended to be attracted by fungal odours alone, but were caught in about ten times higher numbers in trunk traps than in odour traps with the appropriate host. In addition to the species utilizing fruiting bodies for breeding, a specialized spore feeder, the cryptophagid *Pteryngium crenatum*, was also significantly attracted to the traps with chopped *F. pinicola*. Its attraction to intact fruiting bodies seemed still stronger, as indicated by the fourfold catch in trunk traps.

Of the attracted species living on fungi other than polypores, the proportion associated with basidiomycetes growing on the ground exceeded the proportion associated with fungi on wood. Few species associated with moulds or slime-moulds were attracted (Table 6). Two saprophagous beetles, *Nicrophorus vespilloides* and *Sciodrepoides fumata*, were also attracted to the baited traps. According to the literature they are mainly associated with small carcasses, but *N. vespilloides* may also be mycetophilous. The attraction was probably due to the production of substances generally asociated

Table 3. Number of species attracted to the different polypore baits (cf. Table 2) grouped according to the kind of substrate these species are associated with. Species that showed significant attraction to a given bait at at least one locality and showed the same tendency at the other are considered to be attracted to that bait. One taxon for which patterns differed between localities is excluded, as was another taxon with an unknown substrate association.

Substrate-utilization category	Host	Attraction pattern				
		pi	fo	pi = fo	*n. s.*	Total
Polypores	*Fomitopsis pinicola*	3				3
– ″ –	*Fomes fomentarius*	1				1
– ″ –	polyphagous	1				1
– ″ –	*Trametes* spp.				3	3
Other fungi		7	3	1	15	26
Under decaying bark	deciduous	1	4		3	8
– ″ –	deciduous/coniferous			1	6	7
Decaying wood			1	1	12	14
Recently killed trees					8	8
Saprophages				2	2	4
Other substrates					18	18
Total		13	8	5	67	93

with the decomposition of organic matter. This suggestion is further supported by the fact that catches of both species were highest in cases where the bait had been in the trap for more than a week (Table 7).

When changing the substrate after two weeks we observed that microfungi had started to grow in considerable amounts. This could have affected the response of beetles, in which case we should expect differences in trap catch between weeks when the substrate was less than a week old and weeks when the substrate was older. In addition to the age of the substrate, weather and the flight activity of the insects also change over time. For species with a short flight period it is impossible to distinguish effects of substrate decomposition from those of weather and the timing of species-specific flight periods. Thirty-five species were considered to have long enough flight periods and to have been caught in high enough numbers to allow analysis of temporal variation in trap catch. Eight of these species were caught in significantly higher numbers during first weeks (i.e. relatively fresh substrate), and for another eight species the trap catch was significantly higher during second weeks (i.e. decomposing substrate), (Table 7). Most of the species occurring in higher numbers at fresh substrate belonged to the categories living on fungi other than polypores or living under decaying bark on deciduous trees. Species that were more numerous in traps with older substrate were associated with various substrate types.

4. Discussion

Several species of beetles were attracted to the odours of chopped fruiting bodies. However, our comparative analysis of weekly catches indicated that attraction was partly affected by temporal changes in substrate quality. We also noted that microfungi started to grow on the chopped fruiting bodies. This brings up the question of whether the observed responses to the odours of chopped fruiting bodies provide relevant information concerning the in-flight orientation to the odour of polypores colonized by insects under natural conditions. The answer will depend in part on the successional stage of the fruiting bodies that a given species colonizes. There are only a few reported examples of insects attacking vigorous fruiting bodies of perennial polypores (Matthewman & Pielou 1971). For example, cisids are almost exclusively found in dead fruiting bodies (Graves 1960, Paviour-Smith 1960, Matthewman & Pielou 1971, Lawrence 1973, Klimazewski & Peck 1987, Thunes 1994). It ap-

Table 4. Numbers of specimens caught in odour traps (cf. Table 2) of the beetle species that most frequently occurred in the rearings. Asterisks denote significant attraction compared with control (* = $p < 0.05$, ** = $p < 0.01$, *** $p < 0.001$; cf. Table 1). The rearing figures are based on 214 fruiting bodies of *Fomitopsis pinicola* from the spruce locality and 108 fruiting bodies of *F. fomentarius* from the birch locality.

Species	Percentage of fruiting bodies with the species (%)	Numbers attracted at the spruce locality			Numbers attracted at the birch locality		
		pi	fo	empty	pi	fo	empty
Reared from *F. pinicola*:							
Cis glabratus Mellie	64	122***	10	3	6	0	0
Cis quadridens Mellie	33	82***	4	0	2	0	0
Dorcatoma punctulata Muls & Rey	8	8	2	1	0	0	0
Cis bidentatus (Ol.)	7	3	0	0	3	4	2
Ennearthron cornutum (Gyll)	5	21**	6	0	2	1	1
Reared from *F. fomentarius*:							
Cis jacquemarti Mellie	44	1	0	0	0	1	0
Bolitophagus reticulatus (L.)	14	0	0	0	1	0	0
Ropalodontus strandi Lohse	13	1	0	0	1	0	0
Cis alter Silfv. (=*nitidus* (F.))	12	0	0	1	1	1	0
Dorcatoma robusta Strand	5	0	0	1	11*	7	2

pears that perennial polypores have some kind of defense since they can live and sporulate for up to tens of years (Niemelä 1986). A wide variety of secondary metabolites are present in fungi, although not much is known about their effects on insects (Martin 1979). A chemical defense against insects has even been disputed for perennial polypores (Lacy 1984). Because most insects seem to colonize recently died or dying fruiting bodies, we consider it biologically relevant to test the attraction to chopped fruiting bodies, although one must be aware of the fact that certain properties of this odour may rapidly change.

The strong attraction of cisids associated with *F. pinicola* found in this study implies that these beetles can readily recognize the host odour while in flight, which should enhance success of the colonizing process. Although taxonomically and biologically closely related cisid species were abundant in the fruiting bodies of *F. fomentarius*, these species were caught in very small numbers in odour traps as well as in traps beneath living fruiting bodies. This was also the case for the tenebrionid *Bolitophagus reticulatus.* Since the biology of cisids living in *F. pinicola* and *F. fomentarius* are similar, we cannot explain the striking difference in attraction to odours of similarly treated host material.

Another pattern of attraction was shown by the two *Dorcatoma* species: They were not significantly attracted to the odour of chopped fruiting bodies of their hosts but were caught in considerable numbers in traps beneath living fruiting bodies. Also Kaila et al. (1994) trapped high numbers of *D. robusta* at living *F. fomentarius* fruiting bodies. In North America, larvae of *Dorcatoma dresdensis* were found in both dead and living fruiting bodies, indicating that this species is a more primary colonizer than the cisids (Matthewman and Pielou 1971). If the *Dorcatoma* species included in this study also utilize living fruiting bodies, that might explain why they responded so poorly to decomposing material. Moreover, the high numbers of *Dorcatoma* specimens caught in traps beneath fruiting bodies could have been due to pioneer individuals attracting other specimens by emitting a pheromone. Pheromone attraction is well known in anobiids, e.g. in the cigarette beetle (Levinson &

Table 5. Catches of some polypore-associated beetles in polypore odour traps (cf. Table 2) and in trunk window traps placed beneath living fruiting bodies of corresponding polypore species. Although both trap size and trapping periods differ for the two series (see Materials and Methods), relative catches can be compared between species. Asterisks denote significant attraction to odour traps compared with unbaited controls (** = $p < 0.01$, *** $p < 0.001$; cf. Table 2).

Host association and beetle species	Mean catch per trap: Odour trap	Mean catch per trap: Trunk trap
Spore eater on *F. pinicola*[1]		
Pteryngium crenatum	5.3***	20.7
Breeding in *F. pinicola*[1]:		
Cis glabratus	10.2***	11.3
Cis quadridens	6.8***	4.6
Ennearthron cornutum	1.7**	0
Dorcatoma punctulata	0.6	7.7
Breeding in *F. fomentarius*[2]:		
Doracatoma robusta	0.6	6.4
Cis jaquemarti	0.1	1.8
Cis alter Silfv. (=*nitidus*)	0.1	0.1
Bolitophagus reticulatus	0.0	1.4
Ropalodontus strandi	0.0	0.8
Breeding in annual polypores[3]		
Cis boleti	0.7	0.65
Cis hispidus	0.5	0.15

[1] Only traps with or at *F. pinicola* fruiting bodies at the spruce locality.
[2] Only traps with or at *F. fomentarius* fruiting bodies at the birch locality.
[3] Traps with or at *F. pinicola* and *F. fomentarius* fruiting bodies at both localities.

Table 6. Numbers of species associated with fungi other than polypores that were attracted to the different polypore baits (cf. Table 2). Substrate and host association data are more precise than those presented in Table 2. Only species taxa are included, making the number of taxa lower than in Table 2 (*Corticaria* spp., *Atomaria* spp., and *Cryptophagus* spp. excluded). Host data from Palm (1959) and Benick (1952).

Substrate	Host	Attraction pattern: pi	fo	pi = fo	*n.s.*	Sum
Fungi in wood	Moulds			1	6	7
	Myxomycetes	1	1		3	5
	Basidiomycetes		1		2	3
Fungi on the ground	Moulds	1			2	3
	Basidiomycetes	4	1			5

Levinson 1987). Such a scenario, with more or less random searching followed by attraction to a pheromone, is similar to the one suggested for cisids by Lawrence (1973). However, as mentioned above, we found strong host attraction in at least some cisid species.

The insect fauna of annual polypores differs considerably from that of perennials. Almost no cisid species are found on both annual and perennial polypores (Paviour-Smith 1960, Lawrence 1973). Two species living in annuals, *Cis boleti* and *C. hispidus*, were the most common cisids in our control traps and in unbaited window traps in northern Finland (Siitonen 1994), but they were not attracted to our odour traps. The relatively large catches in the controls can be ascribed to the high flight activity of these species, as the annual polypores were considerably less abundant than the perennial ones in our experimental areas. The high flight activity in these species may be related to the shorter life span of their hosts (Southwood 1962).

Table 7. Preference for fresh (first week) *vs* old (second week) polypore baits (binomial confidence intervals, $p < 0.05$). Substrate categories denoted as in Table 2.

Species	Polypore bait preference: fresh	old	no pref.	Substrate association
Calathus micropterus			X	O
Agathidium varians	X			F
Nicrophorus vespilloides		X		S
Sciodrepoides fumata		X		S
Scaphosoma agaricinum			X	F
Lordithon lunulatus	X			F
Biblioporus bicolor			X	B
Athous subfuscus			X	O
Melanotus castanipes			X	W
Dalopius marginatus		X		O
Dasytes plumbeus	X			O
Glischrochilus hortensis	X			B
Arpidiphorus orbiculatus			X	F
Rhizophagus parvulus	X			B
Pteryngium crenatum		X		P
Cryptophagus abietis			X	O
Cryptophagus spp.			X	O
Atomaria subg. *Anchicera*	X			F
Atomaria s. str.			X	F
Dendrophagus crenatum			X	B
Triplax aenea			X	F
Orthoperus spp.			X	O
Lathridius consimilis			X	F
Enicmus fungicola			X	F
Enicmus rugosus		X		F
Enicmus testaceus		X		F
Aridius nodifer			X	F
Salpingus ruficollis	X			B
Salpingus planirostris		X		B
Anaspis rufilabris	X			W
Xylita laevigata			X	W
Anthribus nebulosus		X		O
Total number of species	8	8	16	32

Among the more general fungivores, 10 out of 23 species were attracted to the odour baits. A further division of this group revealed that all five species associated with basidiomycetes on the ground were attracted to the odour baits. Fruiting bodies of basidiomycetes on the ground are very ephemeral, and insects living on them are rarely host specific (Hanski 1989). Fungi on wood are generally less ephemeral, and the associated insects may therefore be more host specific and discriminate better between different kinds of fungal odour. Another group of beetles showing attraction to the polypore baits were species living under bark on dead deciduous trees. This group may be attracted to baits because the odour of the decomposing fruiting bodies resembles that of rotten wood infected by fungi. It is also possible that the wood-inhabiting species are actually more dependent on the fungi as a source of food than on the dead wood itself.

As discussed above, it is possible to propose sound biological explanations for why certain groups of beetles were attracted by polypore odours: They were either restricted to polypore hosts, generalistic fungivores, saprophages, or living under the bark of dead trees, where polypores are likely to be growing. It is more difficult to draw conclusions based on results that were not significant owing to small sample sizes, etc. Nevertheless, we consider the complete absence of any significant attraction among litter-dwelling and leaf-eating beetles and species living in trees that have recently died (Scolytidae) as a true reflection of the fact that these groups do not utilize polypores as food or breeding substrate or as cues in orienting to their primary resources.

A response in flight to odours from potential breeding substrates was found in a few of the species studied, e. g. the cisids associated with *F. pinicola*. If this orientation ability is accompanied by a strong flight capacity, these species should be able to colonize resources that are sparsely distributed in the landscape. Very long dispersal distances have been reported in many beetle species breeding under the bark of recently killed trees (Nilssen 1984) and species attracted to forest fires (Evans 1962). These species depend on more or less unpredictable resources, which usually can only be colonized during a single season. In contrast, perennial polypores on trees are usually available on a continuous basis within natural forest stands. Thus it can be inferred that selection for long-distance dispersal should have generally been weaker in associated insects. Populations of species might therefore be subject to sharp declines in cases where their substrate has become widely scattered. There is, however, no information on the dispersal capacity of these insects. Such data are needed for evaluating the effects of forestry and landscape management on these insect groups.

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